THE

JOURNAL OF GEOLOGY

JANUARY–FEBRUARY, 1901

PROBLEM OF THE MONTICULIPOROIDEA. I.

THE Monticuliporoidea, comprising the greater part of the so-called Paleozoic Bryozoa, are a comparatively neglected group of fossils, as evidenced in such ways as frequent omission or slight mention of them in lists of fossils or descriptions of faunas. They are not, however, really without great scientific value, but rather their unpopularity may be due to the fact that at present there is a real difficulty for the amateur, the collector, or the geologist in making use of them; this difficulty being magnified, moreover, by a too readily accepted supposition that these fossils are for none but gifted specialists to study. In fact, the specimens themselves are very often excellent, the species quite easy to learn or to identify, and well worthy of consideration as to scientific value in geologic faunas, and the entire group is of peculiar interest to biology.

Aside from the retarding supposition that the Monticuliporoidea are difficult, the present difficulties attending them are these: (1) the interpretation of the animal that built the honeycomb-structured organic remains is still uncertain; (2) the monographs in which they are described want censorship; (3) study of the fossil involves technique more or less. These obstructions are, however, not absolute. It is the aim of this discussion to render them better understood, and hence less feared.

Regarding their interpretation, uncertainty exists to the extent that all Monticuliporoidea may be contested as not true Bryozoa, but Tabulata or Alcyonarian corals, belonging then to a different subkingdom of animals. This uncertainty may be illustrated as to its attendant difficulties by reference to Eastman's[1] *Text-book of Paleontology*, Vol. I, where *Prasopora, Neuropora*, and many other genera appear twice, first under Cœlenterata and second under Bryozoa; the first following the text of Zittel, the second the authority of the translator's collaborator, who has taken the liberty to make some revision.

The fact that one cannot assert positively that species of the genus *Prasopora* and other genera were Cœlenterates or were Bryozoons, is due to outward similarity of these two groups and obscurity in the fossils as to class characters. Yet structural details as to minor characters are well preserved, and hence the distinction of species and their grouping into genera is not impracticable here more than in many other groups, since species may be distinguished clearly in fossils as in living organisms without knowledge of phylogenic relation to other classes. Ulrich, who considers them all as Bryozoa, and Nicholson, who treated them as corals, ought nevertheless to present the same determinations as to species, genera, and families. Their failure to agree is not due to that cause. However, the former, in Eastman's translation of Zittel (*op. cit.*), presents as families of Bryozoa (viz., Calloporidæ, etc.) those which, following Nicholson (*vide op. cit.*, pp. 103–105), are given as genera Callopora, etc., of Cœlenterata. Understanding this discrepancy, the handbook is as useful respecting these as other groups, and the fossils are as easily used under its guidance. The student may choose his authority or follow a happy median course.

The lack of censorship in Eastman's *Paleontology*, just mentioned, may serve to argue further need of it in other places. S. A. Miller's catalogue[2] divides the Monticuliporoidea species

[1] Text-book of Paleontology, by KARL A. VON ZITTEL, translated by Charles R. Eastman, 1900.

[2] S. A. MILLER, North American Geology and Paleontology.

between Cœlenterata and Bryozoa. Of other chief works, especially those of Nicholson,[1] we may trust E. O. Ulrich to have criticised them fully. They are conservative and excellent, but inadequate for the study of American fossils without the magnificent recent monographs by E. O. Ulrich[2] to supplement them. The last named, together with the chapter on Bryozoa in Eastman's *Paleontology*, would have offered a complete solution to the student for the study of the fossils and the involved problem of their affinities, if it were not for much obscurity in his definitions. One is compelled to criticise and to interpret anew from the fossils when endeavoring to follow him. In this connection it should be said also that the severe criticism of E. O. Ulrich, by S. A. Miller, *op. cit.*, while touching his works on Paleozoic Bryozoa, does not appear to reach by censorship of the species this group as much or as well as other ones, for the reason, evidently, that his knowledge of them did not permit him. Therefore, while all species are listed as equally valid, some will be found, nevertheless, to have been made upon wholly insufficient evidence and require to be freely eliminated. The most species will again be far easier to identify than their descriptions would lead one to expect. It appears, in short, necessary to admit the value of some earlier criticism[3] of this author, and to expect to find similarities and differences described with acuteness, while fanciful values are frequently attached to them.

Regarding the handling of fossil Monticuliporoidea, one should collect all specimens and in the laboratory select the better preserved ones to begin with. These may be assorted and identified by means of external characters. A common hand lens will suffice to reveal whatever may be not clear to the naked eye. To be sure, the exhaustive study of the material requires the making and use of thin sections when practicable, for often only by that means can the also important internal

[1] H. A. NICHOLSON, On the Structure and Affinities of the Genus Monticulipora 1881.

[2] Geol. Surv. Ill., Rept., Vol. VIII, and Geol. Surv., Minn., Final Rept., Vol. III.

[3] ROMINGER, Amer. Geol., Vol. VI, pp. 103 and 120, 1890.

structure be discovered. The use of thin sections is, however, necessarily limited to special cases. These would be when a new species is in hand and all characters possible should be discovered; or, when a described species is illustrated and described chiefly as to its internal structure, which too frequently is the case; or, when the external characters have been obliterated. Having identified the species and referred it to a genus, etc., by use of all characters, further recognition of specimens of the same can and should, with rare exception, be made to depend on external characters alone. As in studying Brachiopoda, for example, one must know them by external characters, even though examination of internal structures is required to determine affinities of the species.

The advantage of learning to recognize the species, genera, etc., by external characters is in the saving of time, since thousands can be examined in that way, while sectioning limits the labor of one man to at most twenty specimens per day; knowledge of the range and variability of one and many species is made practicable; it serves to direct to best advantage the use of thin sectioning; recognition of species even in the field becomes thereby entirely practicable. Having learned to know a group of species, or the fauna of a locality or of a zone, the specimens may be identified thereafter without the use of sectioning, and the difficulty of technique may be obviated by the geologist.

Thin sections of fossils may be made by the same process as bone or rock sections are ground, which need not be described here. It requires less skill, however, since they should not be ground to absolute thinness. Some simple appliance for measuring the cell dimensions is also needed.

Pains may be saved by attention in collecting, since each bed or zone may have a large proportion of species peculiar to it, and by avoiding mixing fossils of different zones, labor of again assorting is saved.

TREPOSTOMATA

A few selected species may illustrate what is to be looked for in Monticuliporoidea. Beginning with Trepostomata one

then has to do with the most problematic as to affinities of the so-called Paleozoic Bryozoa, *i. e.*, those which most resemble corals, proceeding then to those often supposed to be true Bryozoa, the Cryptostomata. Eastman's manual, *op. cit.*, includes them in the arrangement given below, and in the Order Gymnolæmata, which comprises most Bryozoa and all known fossil ones. Of those five divisions, the last named, Chilostomata, are all undoubtedly Bryozoa, but are not known in the Paleozoic rocks. The first, Cyclostomata, are, with few possible exceptions, all true Bryozoa, but few of them are Paleozoic. The second, third, and fourth comprise the Monticuliporoidea.

1. Cyclostomata (8 families).
2. Families doubtfully referred to Cyclostomata (4 families).
3. Trepostomata (7 families).
4. Cryptostomata (8 families).
5. Chilostomata (13 families).

In that arrangement those of doubtful affinities are embraced between the true Bryozoa. A fairer presentation of the problem may be given thus:

Tabulata (corals)——Trepostomata (?)——Cyclostomata (bryozoa)
|
Cryptostomata (?)   Chilostomata (bryozoa)

and it is in such association that the Monticuliporoidea should be studied. The group of "Doubtfully referred to Cyclostomata" are Trepostomata.

Beginning with one of the simpler Trepostomata,

Monotrypa magna Ulr. has a skeleton or zoarium one or two inches in diameter, composed of tubes or "cells" which radiate from an approximate center. It is nearly spherical if growing attached on one point, or discoid if on a flat surface, or, again, irregular. The center is the initial or oldest part, and from it one, or practically several, cells arise, and as these extend, others intercalate successively. A specimen divided radially (Pl. A, Fig. 2) shows parallel, approximately equal, cells, each tapering to a point at the inner end. The plan of growth is that of increase in number of cells proportionate to the increase in size of the zoarium. At the surface, the open cell ends are

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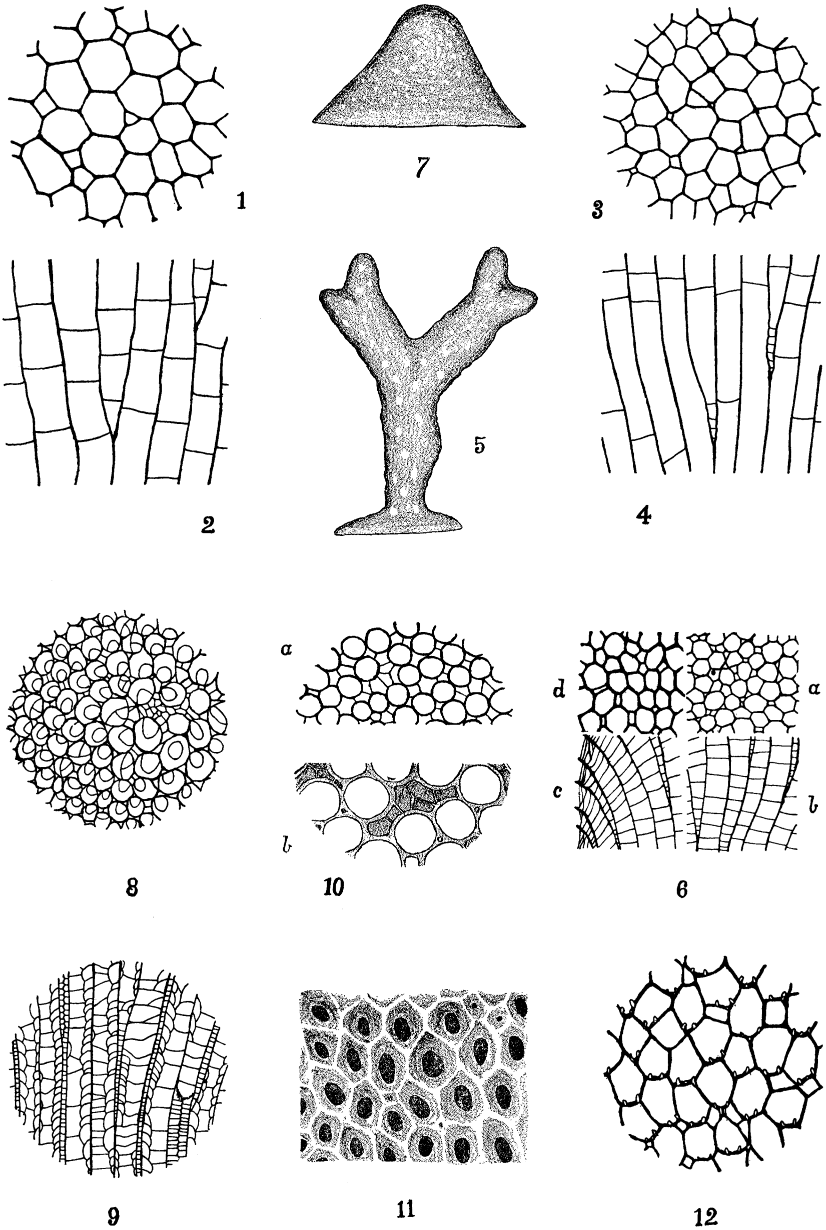
Plate A



approximately equal, and, like the cell throughout, are polygonal or hexagonal by reason of contact (Pl. A, Fig. 1). The incipient or expanding parts of cells are seen there as small tri-, or quadrangular openings at the angles between the older, larger cells. Crowding of the cells appears to prevent entire regularity in shape and size of each cell, and the walls are crenulate.

In speaking of cell one includes for each the half of the bounding wall, although the walls originally are dense, amalgamated, calcareous structures, not double further than that they were built not only by increment upon their margins, but also on the two surfaces. Theoretically there is a boundary plane or division between cells midway in the wall. They frequently split midway in the wall when fractured. The walls in this species are thin and show little or none of their growth structure. At a slight depth within each cell the last growth increment or layer crosses the cell opening and forms a transverse partition or false bottom, the so-called tabula. Tabulæ occur successively in all cells more or less regularly, but not corresponding in neighboring cells. They are a little more numerous in the incipient part of each cell. The wall edge of one cell cannot extend above those of its neighbors, from which it never separates.

The zoarium corresponds in structure to the following supposed manner of growth: It was covered when alive by numerous equal sized zooids which coalesced laterally, the lower part of each, however, extending into and secreting the walls forming the cell or zoœcium. Young zooids arose among them and, growing, extended relatively downward, building a new cell; the increase in number of zooids and, respectively, cells, being compensated by a necessary growth in radial length of cell wall to increase the surface of the inhabited zoarium. The tabulæ indicate successive planes where the bottom of the zooid rested between periods of necessitated self-extraction from the ever too long cell.

E. O. Ulrich assumes that the cells are "Zoœcia, directly superimposed upon one another so as to form long tubes

intersected by straight or curved partitions . . . ." That interpretation appears in form of a definition only; and not knowing how it could be applied to the initial part of cells, respectively young zooids, which then must be supposed to have required several generations to reach maturity, the other interpretation will be kept for the present, viz., that each cell is one zoœcium.

Variation in such species as this one would consist in the zoarium growing in one part more than another for some cause, being one-sided; or it is discoid because of perigene growth, *i. e.*, the cell increase is greatest around the margin; or, again, it is acrogene. The surface upon which it grew affected its growth also. The cells remain nearly uniformly large, the number of young cells seen at the surface varying. The cell walls appear uniformly thin.

Those characters are seen at the surface or in transverse thin section. Longitudinal section would show the tabulæ to vary, being fewest where cell length most rapidly increased, and the slightly differing rates of expansion of the cell initial. The atter character can also be estimated at the surface. Other species near to this one are in various ways more complex. Thus,

Diplotrypa limitaris Ulr. has nearly the same manner of growth as *Monotrypa magna*, differing in smaller size of cells and shapes of their apertures at the surface (Pl. A, Fig. 3). Here the number of immature cells nearly equals that of the mature ones. Longitudinal section shows that the young or initial part of each cell is long, slowly expanding, or even for some length not increasing, then quite quickly becoming full-sized, mature (see Fig. 4). The tabulæ are closer in these initial parts, technically called *mesopores*. The plan of growth thus differs from that of *Monotrypa magna* in that in the latter new cells appeared only as fast or numerous as they were to develop into mature cells. In *Diplotrypa* the new cells appear too rapidly, so to speak, and await their turn to expand into full size; hence the more

numerous small cells, mesopores, among the full-sized autocells at the surface. The calycal or open part of the cell is shallower in small cells or mesopores than in the larger ones, and that is true in all Monticuliporoidea. Also the autocells crowd the mesopores so that the former tend to become circular at the expense of the latter.

Callopora multitabulata Ulr. began like a *Mesotrypa*, but acrogene growth obtained (Pl. A, Fig. 5), the zoarium being long, cylindrical, branched, arising from a basal discoid expansion. The tips, or apices, are only then like small *Mesotrypa*. The greatest growth of zoarium and cell increase was at the zoarial ends, and there the cells increase centrally, so that some were being crowded away and turned their apertures to the peripheral surface, *i. e.*, away from the axis of growth (Pl. A, Fig. 6, *c*). The grown zoarium is thus composed of two regions, the axial or "immature" region of vertical cell part (Fig. 6, *b*, *a*), and the peripheral or "mature" of laterally directed cell (Fig. 6, *c*, *d*). In the peripheral region the cells grew slower in length, have thicker walls and more numerous tabulæ, and there are more mesopore cells. The apical parts also become finally slow-growing, thick-walled, with many tabulæ and many mesopores, and it is evident that the zoarium grew rapidly to nearly full size; then a retarded or "mature" growth followed. Renewed rapid zoarial growth and a second retardation stage often occurs, wherefore the terms immature and mature regions are presumptious terms. Peripheral and axial regions are better, since they leave the degree of maturity to be described. Upon the thick-walled peripheral and apical part there occur at nearly regular intervals elevations called monticules. These are occupied by a small group of larger-sized, cells with mesopores or young cells. On the thin-walled or growing apex, and hence in the axial region, these are represented by a group of likewise slightly large-sized cells, with abundant mesopores, resembling less distinct cell groups occurring in *Monotrypa*, etc. Nicholson proved monticules to be points of greater cell increase, and while

young cells may appear at any cell angle, their increase is greatest in the monticules or cell groups. In renewed rapid growth the peripheral monticules tend to develop into branches of the zoarium, but of course all could not. Thus monticules are similar to zoarial branches, but are not branches normally. Branching of the zoarium is due to double region of acrogene growth only.

The tabulæ of *Callopora multitabulata* are thin, and the last one is near the cell aperture, and is said to be perforated at the center (*vide* Eastman, *op. cit.*, *f*, 456 *d*). They are nearly always solid. Right here is the chief supposed basis for the interpretation of Trepostomata as Bryozoa. According to E. O. Ulrich's definition (p. 271, Eastman), each tabula was the perforated top of one zoœcium and solid bottom of the next. In fact, the thickened walls here show only that the growth increments lengthening the wall continue on either side downward, thickening the wall, and thence as tabulæ across the cell opening. Further is not seen. Perforate last tabulæ may be incomplete ones.

The characters for distinction of the species are, therefore, mostly visible on the exterior; the shape of zoarium and its branches, shape, size, and shallow depth of the cells, characters of the monticules, the number, size, and shape of mesopores, and thickness of the wall. All these characters vary, and the variation of all should be noted in learning the species. Extremes may be associated on parts of the same specimen.

Prasopora simulatrix Ulr. grew upon some solid surface, at first lens-shaped, later conical (Pl. A, Fig 7), hemispherical, or irregular, expressing slight tendency to acrogene growth, united with moderate established perigene. A short finger-shaped or a branched sporadic acrogene growth occurs sometimes, and this usually at the center. If the colony died off in part, the remaining part then developed, overspreading the old. Even a symmetrical zoarium could develop from the irregular fragment of another. The cells radiate from the flat or concave lower

side to the convex upper one, the lower side being covered, if well preserved, by a thin "epitheca" or coating produced by no one zooid, but by the cortex uniting all. The growth of the epitheca was, of course, marginal. At this margin, close on the epitheca, there was rapid budding of young cells, some of which became quickly full-sized; others became mesopores. At the periphery the cells open obliquely to the zoarial surface. Above it all apertures are more direct.

The number of mesopores in this species (Pl. A, Fig. 8) is so far greater than that of the autocells that relatively few of them can become autocells. They are fewest proportionally in maturer zoaria, and appear to be homologous with those of *Diplotrypa*, only smaller, longer, and, so to say, more permanently mesopores. The numerous small, angular, or impressed mesopores, with shallow openings or calycals, surround the rounded apertures of the thick-walled autocells, making an easily recognized figure at the surface. At intervals occur clusters of cells larger than the average, with more numerous mesopores between them, and thicker walls. They form low monticules, or on weathered specimens high ones. They are areas of rapid cell increase.

The mesopores have numerous transverse tabulæ (Pl. A, Fig. 9). Those of the autocells are numerically proportional, considering the cells' size, but they curve obliquely across, or oftenest form cystiphrams, *i. e.*, the tabulæ in the most regular instances are narrowly beaker-shaped, and are arranged in the cell as nested equal-sized beakers could be in a tube. The flat bottoms have been called diaphragms or tabulæ, the sides cystiphrams. Often the cystiphram extends only partly around the cell, and partly the same lamina is incorporated with the cell wall. Cystiphrams appear to indicate that the zooid body withdrew simultaneously, or nearly so, from the calycal bottom and side, or sides, near the bottom.

The cell wall margins here were not all straight since, *acanthopores* occur. These are minute wart-like structures or thickenings on the cell wall margins, especially at angles, and were

presumably built into corresponding invaginations of the living cortex. They are not cells or pores, but have been supposed to be, hence the name. They are inconspicuous in this species or even wanting, and will be discussed later.

Characters sufficient for the determination are upon the exterior in this as in related species. The peculiar cell pattern can be readily distinguished from structurally very similar ones. The variability in cells, acanthopores, etc., will however be found greater, and there are fewer true species of the genus than recorded. Other species of *Prasopora* have more perigene growth, or, again, acrogene ones are the *Monticulapora*.

Homotrypa minnesotensis Ulr. has long, round, slowly-branching zoarium, with many specific marks as to cells, monticules, etc. Fossil stems are in part or entirely hollow, because the axial region has very thin crenulous walls without tabulæ, hence the sea water could enter and eat away the walls, leaving, if anything, the thicker-walled tabulate peripheral region. The peripheral cell has cystiphrams similar to *Prasopora*.

Batostoma fertile Ulr. consists of large, flattened, or round, somewhat irregularly branching acrogene parts, arising from a large basal expansion of irregular perigene growth. A single basal may support more than one or, again, no acrogene part; but as in *Callopora* a thick walled maturity follows the thin walled, immature stage. Thus the characters of peripheral and axial regions are evident when there is even no acrogene growth. Omitting some details, the peripheral region has thick walls on which are well-developed spines, acanthopores. Mesopores may be very few or, again, very numerous on parts of the same specimen (Pl. A, Fig. 10, *a*, *b*). They are "closed," *i.e.*, their tabulæ built close up to the apertural margin, by which the mesopores, being shallow or confluent, look like closed interspaces merely between the rounded autocells. The cell clusters, which are in place of monticules, have *maculæ*, *i. e.*, clusters of mesopores at their center. The young cells of the axial region

expand quickly, and are scarcely tabulated and very unlike mesopores of the peripheral region, and they are not called mesopores. The mesopores of the axial region are not immature cells but permanently retarded ones.

With this species is conveniently compared *B.* (*Hemiphragma*) *ottawaense* Foord, in which the thin-walled axial and thick-walled peripheral regions are sharply defined, as seen in thin section or in fractured specimens. At the stage when peripheral region is just begun one sees characters very like *B. fertile*, but later the walls thicken more, the mesopores are obscured, closed, or filled, while the maculose-looking monticules show strongly diverging cells, indicating slow growth in cell length compared to width. Acanthopores developed. The tabulæ are peculiar, being often thickened and incomplete, hemiphragms, in the peripheral region. The whole wall in the fossil is corneus looking. They show the result of a decrease probably of calcareous constituent.

Eridotrypa mutabilis Ulr. includes rather small, long, branched, acrogene zoarial parts in which, as seen in cross fracture or section, the cells are larger in the axial region than in the peripheral. The cells turn very slowly in the peripheral region, so that the apertures are oblique to the surface and drawn out anteriorly. Then, as the cells become more direct, the walls increase steadily in thickness, and in very "old" specimens distinctly cup-shaped calycals form (Pl. A, Fig. 11). The thickened wall permits analysis into the bounding edge with its projection downwards, as dividing lamina, and the calycal slope and the main wall below it (*cf.* Fig. 1, *h*, *p.* 21).

Anolotichia impolita Ulr. has irregular large acrogene zoaria, with large cells of quadrangular rather than polygonal outline, and with few mesopores, reminding of *Monotrypa magna* (Pl. A, Fig. 12). The axial and peripheral regions are scarcely distinguished. In the latter stage there are, however, *lunaria* developed. The lunarium occurs in the posterior side of a full-sized cell as a narrow, distended part of the cell. The term lunarium has been applied rather to the lunarial wall, which is narrowly arcuate or crescentic. Where the lunarial and common cell walls join, in

this species, the angles project inwards, as if produced. Moreover the lunarial wall is a little elevated at the surface, making it appear as a distinct wall, but it is really part of the wall deflected and extended. I have searched in vain for the symmetrical crescent that has been figured as the lunarial structure of this species. It appears really to be somewhat irregular, bearing tooth-like points, the downward projections of which appear lucid in thin sections, and are the "vertical, closely-tabulated tubes" described by the author of the genus and species. These same lucid spots in sections crossing calcite-filled cells are very deceptive, appearing like pores. In clay-filled cells they appear clearly as parts of the wall. They interrupt the median wall and confuse in color with the outer laminæ, these lighter parts being also of the same color as calcite infiltration; hence the deception in the fossil.

Fistulipora carbonaria Ulr. is of common, massive growth. Its autocells are rounded, with here and there one having a slight distension, as if a lunarium was developed with minimum distinctness. The autocells are separated by angular, large mesopores in single series, except in the clusters or maculæ, where they are more numerous. The walls around autocells are thick, while those between mesopores are very thin, low, and scarcely above the last tabulæ; hence the appearance is that of isolated autocells with raised "peritreme." Longitudinal section shows the mesopores to have arched, numerous tabulæ, appearing thus as vesiculose filling, or "cœnenchyma" between the autocells. New autocells arise abruptly, displacing one or more mesopores in the midst of mesopores, *i. e.*, "cœnenchymal gemmation."

Stellipora antheloidea Hall encrusts shells, etc., growing laminar or massive, a centimeter thick. The surface is crowded with stellate monticules about 2.5^{mm} wide, each consisting of a central, six to twelve-rayed, depressed, quite smooth, macula, and around this, between its rays, an equal number of ridges which are highest at the inner end and slope outward to the interspace. Sometimes additional ridges occur midway between the outer ends of the primary ones. The maculose

area, as proved by sections, is composed of large, angular mesopores, and the ridges exclusively of rounded autocells, these tending to arrange in two rows, with the walls between the rows a little raised and straightened. The space between monticules is small and occupied by mesopores around a few single autocells, and groups of two, three, four, etc., cells or incipient ridges. In longitudinal sections the close tabulæ only distinguish the mesopores at first, but they soon become vesiculose.

This description is taken from specimens from the "Trenton shales" of the Northwest. The species is very rare as compared to the acrogene ones generally called *Constellaria*.

DISCUSSION OF TREPOSTOMATA

A few species suffice to illustrate the general characters of Trepostomata, and the further detail may be explained by them. In this manner of beginning with a few representative species, proceeding thence to the study of the several characters recurring in the whole group, the perplexing taxonomic definitions may be obviated.

The growth habit or zoarial form is fairly constant in the species, but very various beyond that taxonomic limit. The approximately hemispheric zoarium, with its cells radiating and multiplying with growth from an initial point, may be taken as the central or composite or primitive type. Next, species with an established tendency to grow fastest around the base develop the flattened massive type. Others, more perigene in degrees, connect with the laminate or encrusting, in which perigene growth is near its practicable extreme.

On the other hand, the hemispheric form, by increased acrogene growth tendency, becomes the digitate, and finally dendroid branched. But, as a rule, the acrogene zoarium has a perigene basal expansion, and every degree of form might be pointed out from the conical (Pl. A, Fig. 7), in which moderate acrogene and perigene combine, to the strongly acrogene form, with more or less extremely perigene basal (Fig. 5). As to the basal expansion, it may be massive, laminate to encrusting. It

may in some species support two or more acrogene growths, and in just these cases also the acrogene part may be small or wanting, arguing that the basal expansion might have been the origin of some strictly perigene species, the acrogene part being wholly suppressed. The laminate form may have again become massive. Finally, an acrogene growth may be round, compressed, flattened, frond-shaped, or bifoliate. In short, the series between zoarial forms is very complete, and genetic relationship between the most extreme forms may be presumed. The lines of evolutionary development have never been traced, however, and they evidently cross or parallel in a confusing manner; hence this character is of taxonomic use in species chiefly.

The different zoarial forms result not from changed shape and size of the component cells, as one can readily observe in similar zoaria of extremely different cells, but, as seen firstly in variations of a species, it results from increase of cells, the region of greatest cell increase being that of greatest zoarial growth, and inversely. The change of zoarial form, nevertheless, must be made to explain the change of cell as seen in different regions in the same species. Thus, in the acrogene growth, where the cells are turned from the axis of rapid growth to the peripheral slow growth region, it changes markedly, becoming thick walled, closer tabulated, etc. (Pl. A, Fig. 6, *c*). Noticing that the cell apertures do not spring apart under any circumstances, and presuming that this is because the respective zooids were bound together by a cortex, it can be understood how the same cell can be different in two parts, and why there are certain differences in cells. Thus, the tip of an acrogene zoarium, like a hemispheric or massive zoarium, has the cells subparallel, lengthening as new cells develop, so that the surface or circumference widens and the radius or cell-length increases proportionately. But as a cell turns into the peripheral region it comes into a zone of more restricted circumference and radial lengthening; hence the cell is shorter, thicker-walled, and closer-tabulated. Moreover, the cell-increase lessens to some degree, which further restricts the circumference and radius with added effect. In the

latter way the apex of branches often retarded building thick-walled and close-tabulated cells, and sometimes the basal expansions did likewise; and it is evident then that a kind of zoarial maturity exists, simulating if not derived from the "peripheral" stage. Further, specimens in which a mature stage has developed at the apex may renew axial growth and cell characters, a second maturity following, by which it would seem that environmental causes have had to do with the time of maturity.

In a specimen of *Eridotrypa mutabilis* Ulr. at hand, a fortuitous branch has arisen from the mature region instead of the axial, and consequently a cell can be traced as axial, peripheral, axial, and peripheral again. Injured or broken zoarial parts are commonly renewed by thin (axial) cell growth, even in the peripheral region, a stolon-like expansion first overspreading the dead area. In perigene growth also the young cells arising at the margin are at first more prostrate than later, giving rise to a basal stolonal region, and in thin, laminar, or encrusting forms it is very distinct. In these cases the stolonal has been said to be probably the homologue of the axial immature region of dendroid zoaria. The stolonal and immature regions in these may coincide, but it is wrong to assume that they do in other and all cases. The stolonal part need not be considered as coördinate with the developmental peripheral and axial regions. It seems, in fact, unnecessary to attach any genetic significance to the stolonal region further than that it is incidental to perigene growth.

In a given species one specimen larger than the other may be so either from more vigorous growth, as seen in larger axial or immature region, or from longer continued growth, as seen in thicker peripheral or mature region.

Cell increase is, as a rule, intermural, *i. e.*, young cells begin as small, round pits in the wall at the angle between three or more older cells. The reproduction or budding of zooids doubtless took place in the cortex above the zoarial skeleton, and only later the young zooid comes to build a cell, which, however, from its initial, has its own wall, *i. e.*, wall-half. The young cell

becomes triangular, quadrangular, etc., in proportion as it grows large enough to neighbor on three or more cells. Young cells have shallower calycals and are generally closer-tabulated, but proportionate to their size, as compared to mature ones. The number of young cells in proportion to large ones affects the cell pattern at the surface. This is especially notable when the simplest case of rapid, direct, continuous expansion of young cells is contrasted with that where "mesopores" are numerous (Plate A, Figs. 1 and 10).

Mesopores are said to be present if the young cells when about half-grown in diameter, retard or cease their expansion, but, of course, continuing length growth. If the mesopore stage of cell is short, few mesopores, if long, many mesopores, are present. They may outnumber the autocells so greatly that a small proportion only could become autocells. They may be more numerous in the peripheral, mature, or retarded cell growth region. Again, as in *Prasopora simulatrix* many mesopores remain such while other newer ones develop to autocells. Yet, apparently any mesopore may finally become autocell. They are, however, something more than retarded young cells, in case like *Stellipora* (*Constellaria*), where the angular mesopores are rather larger instead of smaller than the rounded autocells.

The more distinct the mesopore development the more subordinate they appear to become. The autocells are angular from contact with each other or young cells, but rounded when crowding mesopores, the latter alone remaining angular. Also the mesopores become shallow, the tabulæ developing close to the wall margin forming "closed" mesopores, or they even filled solid with superimposed tabulæ; or the tabulæ overlap the walls, forming "vesiculose" structure. Autocells arise, displacing several mesopores at once, "cœnenchymal gemmation," in some species with vesiculose or even regular mesopores.

Monticules, as Nicholson pointed out, are rapid cell increase areas. In simplest cases they appear at the surface as mere small elevations or more or less elevated clusters of slightly larger sized cells, among which young cells are seen except

rarely in a growth retardation stage. A few young cells or mesopores are present, or many mesopores, or again aggregated mesopores between the cells are found in some species, or exclusively mesopores form maculæ or large aggregates in other species, with or without surrounding major-sized autocells. The elevated clusters are the typical *monticules*. The extreme degree of elevation is expressed by the name monticule. Maculose ones or "maculæ" are nearer plane or slightly depressed. Exceptionally a typical monticule may extend like a ramulet, in which case it is probably to be considered as such,—a fortuitous acrogene growth having sprung from the area of one monticule as it might also have from that of several.

The monticules are distributed on the zoarial surface more or less regularly, new monticules arising from the widening intervals, and never, apparently, one monticule from another. The function of the zooids that built the major autocells is unknown if it was different from that of others. The only discernible peculiarity of the monticules to which a special function could be assigned is their more rapid reproduction or cell increase than the interspaces. In this respect they resemble the acrogene growths or the axial region, and when very prominent they might suggest an origin as retarded branches, but no unquestionable transitional forms to these are known to me. They differ from branches in their size and in relation to the zoarium as a whole; for, if monticules produce the more new cells, their interspaces produce the less, the zoarium being unchanged; while, on the contrary, growth of branches comprises essentially the zoarial growth as well as the maximum increase of cells.

The surface pattern, as shown, is very diverse. The average size of cells in a species is quite constant, but in different species differs several diameters. The form of aperture, quadrangular, polygonal, to rounded; the relative size and numbers of young cells and mesopores; the monticules and maculæ of varied style; all these form conspicuous essential characters by which species can be recognized. The calycals, too, are deep

or shallow, relatively, in different species. The autocell walls, which are thin and then more or less thickened, give respectively polygonal or rounded calycals, since the thickening is greatest at the cell angles. A beveled wall edge or impressed rim around the cell aperture gives it in many a saucer-shape, especially when the walls are very thick (Plate A, Fig. 11).

Acanthopores or warts may be present on the walls, usually at cell angles. A lunarium, when present, gives the cells another peculiarity. The lunarial wall and the acanthopores are, however, mural modifications, and will be explained in that connection later.

Thin section is quite necessary to bring out the wall's structure. The walls are dense. If thin they may show no differentiation; yet, if a specimen split, the cleavage may pass longitudinally and so as to leave part of the wall attached to each stone core, which fact has been taken to indicate that the wall is always structurally double! Presumably the wall is built double always, *i. e.*, the increment on the margin is continued within every calycal, the wall being thus double with a median, third part, which is, however, not known to be double. A thickened wall tends to show greater differentiation, both in structure and composition, than a thin one. The median wall may appear either distinct or not, and correspondingly the striping parallel to the wall's surface when seen, showing the laminæ of growth, is either interrupted by the median wall or more or less distinctly crosses continuously from one side wall to the other.

To explain the structural aspect of acanthopores in thin sections, the following analysis may serve. A distinctly double wall shows the median wall as a line in transverse section (Fig. 1, *a*) and when the wall edge is scalloped (Fig. *b*) the median line appears interrupted in section (Fig. *c*), corrresponding to the angles. A rounded wart (Fig. *d*) would produce a similar effect (Fig. *e*); or, if very distinct, as in Fig. *f*. When once begun, the wart may have its own growth, so to say, independent of the wall thickness (Fig. *g*), becoming so large as to appear

to have displaced a young cell or mesopore. Such a large acanthopore inflects the cell wall, forming a vertical rib or pseudoseptum as a rule. No doubt the acanthopore end, or wart on the wall, extended to fill an invagination in the web or cortex which bound the zooids to which the cells belonged. Explanation of the cause of such invagination need not be attempted here. But it may be added that the walls were evidently built by surface secretion, and that the growth of a projecting wart would be accumulative as compared to a plane surface, other things being equal. This may explain why acanthopores are

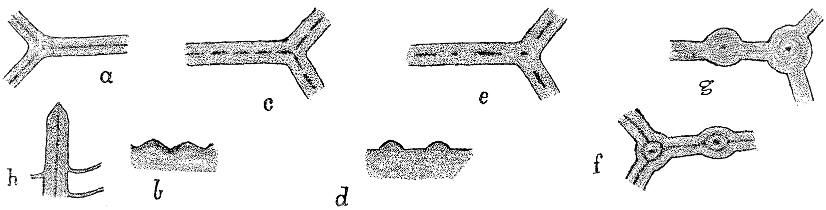


FIG. 1.

often so independently large. A scalloped or saw-edged wall would not develop so. The transverse of a wall would, however, if the zooids and cortex did not draw upwards fast enough to prevent it. Thus a wart thickens in two dimensions to the wall's one. Since, however, the wart is on the wall, it receives below the wall thickness also, and hence acanthopores might well be four or more times the thickness of the wall from result of secretion alone. In fact, it is necessary to explain why the walls, etc., can be very thin, which is evidently because the zooids drew forward rapidly.

It is fair to presume that structural differentiation of the wall may be accompanied by difference in composition; and that may explain why the elevated lunarial wall may be different colored and textured than the main wall; or, again, lucid vertical lines or "lunarial tubuli" only are different, these being the vertical extensions of tooth-like elevations on the lunarial wall margin. Acanthopores show similar differences. Such structures might be mistaken for mural pores in thin sections. Mural pores do not occur.

Tabulæ perhaps need no special mention; their character as the successive bottoms of the calycals is entirely evident (Plate A, Fig. 2, and Fig. 1, *h*, p. 21). In structure, if any be seen, they are one-sided. E. O. Ulrich has observed the very rare occurrence of perforation or circular opening in the last tabula, which he interprets to prove that all other tabulæ are double, comprising the amalgamated cover of one zoœcium and bottom of a next superimposed zoœcium. In absence of any substantiating evidence it is better to take the most direct explanation, which would be that the observed perforated tabulæ were left incomplete by the death of the colony. Indeed, in *Hemiphragma*, the tabulæ of the cells in the peripheral region are all left incomplete or were imperfect as to calcareous structure. The surfaces of tabulæ are sometimes papillated, and these again, like the acanthopores, simulate perforations in the fossilized specimen.

As a rule, neighboring cells do not have corresponding tabulæ, either in position or number. In any species or individual they are approximately regular in position and numbers, but never quite so. In different species the number ranges in extremes from none, as seen in the axial region of some species, to very many in others, or even to a compacted papillose mass filling the cells, or especially the mesopores in some thick-walled forms. There is no unit form and size of loculus assignable, which argues very strongly against any theory that the successive loculi represent superimposed zoœcia. The clearer interpretation is that each cell was built by one zooid. Tabulæ are, as a rule, very thin; and tabulæ wanting and tabulæ thickened are opposite degrees. Individual variation and specific difference in number and thickness of tabulæ may be ascribed to difference of growth and to secretion of substance. Difference in form, such as the cystiphrams (*Prasopora*), are ascribable to shape and size of the zooids' base; and vesiculose mesopores, to shallow or closed calycals from short zooids, and to their shifting, possibly, also.

AFFINITIES OF TREPOSTOMATA

Regarding the affinities of the Monticuliporoidea as a whole, the evidence uniting these to the Bryozoa on the one side, and to Tabulata or Alcyonarian corals on the other, does not lead to a compromise conclusion that they really were related to both as an intermediate or connecting link, because, as will be seen, the interpretation of the zoarium necessary to unite them with the one is discordant to that necessary to unite them with the other; and because of evidence to the contrary from the embryology of living Bryozoons and corals. Discussion is therefore confined to the question whether the extinct Monticuliporoidea are Bryozoa or Cœlenterata.

In relation to Bryozoa, the problem begins with the Trepostomata section, some or all of which have been variously and doubtfully referred to Cyclostomata; and this order of Bryozoa is extant. The reference involves comparison with the supposed Cyclostomatous genera *Neuropora* and *Heteropora*, of which we are yet uncertain. Gregory[1] refers these as typical Trepostomata, not Cyclostomata. The question rests mainly upon the fossil and recent *Heteropora* which Nicholson[2] has thoroughly discussed and which, as it appears, simulates Trepostomata, but has many transverse mural pores and other differences. Trepostomata must therefore be proved to be Bryozoa and *Heteropora* likewise to belong to Trepostomata, before they can be united with assurance. Gregory's reference needs proof and affords no evidence, but expresses well perhaps that we are uncertain of all. Passing to the comparison of Trepostomata with undoubted Bryozoa, this requires knowledge of the extinct Cryptostomata, which must in turn be compared with Bryozoa; and discussion of that part of the problem will therefore be deferred to the section on Cryptostomata.

In relation to Tabulata or Alcyonarian corals, Trepostomata may be compared immediately. In the first place, such forms as *Monotrypa* compare with *Chætetes*, a massive zoarium of small,

[1] Catalogue of Jurassic Bryozoa, p. 193, 1896.

[2] Structure and Affinities of the Genus Monticulipora, p. 62.

tabulated, thin-walled, polygonal cells. *Chætetes* has comparatively lighter colored, probably more calcareous walls. Its cells increase only by fission, while intermural "budding" obtains in *Monotrypa*. It is said, however, that fission occurs rarely in Monticuliporoidea, which leaves a difference in degree only between these two. *Chætetes* is extinct, but is referable only as a coral. It indicates that the *Monotrypa*, *Monticulipora*, etc., are corals; but that the family *Chætetidæ* should contain *Monticulipora* seems doubtful when *Fistulipora* is placed in a family of its own.[1] Certainly *Prasopora* does not belong in both.

Fistulipora, which is the extreme form of Trepostome as compared to *Monotrypa*, is the very one most approaching the Recent coral, *Heliopora*, which, as shown by Mosely, is an Alcyonarian, with a true tabulate skeletal structure. *Heliopora* has the larger cells, but like *Fistulipora* has autocells among mesopores, called siphonopores. The autocells increase by "cœnenchymal gemmation," *i. e.*, a young autocell arises among siphonopores, displacing several. Siphonopores and mesopores are alike. Also, in the mature region of *Heliopora*, the walls thicken and a wart-like projection stands generally at the siphonopore angle and twelve of them surround the autocell. Structurally the warts are similar to "acanthopores," but the wall of *Heliopora* is highly calcareous, and in thin section one sees primarily the crystalline structure radiating from the normal line or center, while the Monticuliporoid wall, being apparently less calcareous, shows the organic lamination, and the acanthopores have concentric structure. The difference is referable to the degree of calcareous deposit in which all corals differ. The warts on *Heliopora* are due to transverse canals between zooids swelling the cortex unevenly. Acanthopores might well be of like origin, and if so they indicate a canal system like that in Alcyonaria.

It has not been clearly enough understood that Mosely[2] demonstrated the *Heliopora* to have no mesenterial septa, but that twelve vertical ribs in each autocell are pseudosepta; and

[1] EASTMAN, op. cit., pp. 102, 103. [2] Challenger Report.

as such they can be compared exactly with the inflections produced by acanthopores in many Monticuliporoids, if the small difference in calcareousness of skeleton be considered. More calcareous ones have sharper processes. A lunarium is wanting in *Heliporidæ*, but this structure is absent in *Fistulipora* in part, and in most Trepostomata. Any structural differences between *Heliopora* and *Fistulipora* are found further in some genus or other closely related to the former, except the monticules or maculæ of the latter.

If one places all Trepostomata and the Tabulata (Alcyonaria) together, they are compared as follows: The largest cells of the former are scarcely equal the smallest autocells of the latter. Growth habit is alike. Cells, monomorphic or dimorphic, are alike; except that distinct pseudosepta in autocells are common in Tabulata, being absent in few cases and these when the walls are very similar in structure to that of Trepostomata, *i. e.*, when crystalline radiate striping is absent,— except also that mural pores cross the walls of many Tabulata, not, however, in dimorphic forms nor in monomorphic ones with small cells,—except again, the lunarium of Fistuliporidæ and the so-called dorsal septum of Alveolitidæ. Notably, the two lunarial angles, forming two pseudosepta, are on the upper side in the former, the single "septum," pseudoseptum, is on the lower side in the latter; the structures therefore not corresponding. If, however, they be ascribed respectively to the double ventral folds and the single dorsal fold of certain Alcyonarian Recent corals,[1] one finds them all represented in Cœnites, a Paleozoic tabulate coral. They are rarely indicated in skeletal structure of either Monticuliporoidea or Tabulata, but argue Alcyoranian affinities.

Cell increase is not unlike. In the Tabulata (Alcyonaria) it is by fission, unequal fission, stolonal gemmation, and intermural gemmation, which are probably degrees of transformation.[2] Intermural gemmation is the rule in Trepostomata. The peculiar

[1] See further, Neues Jahrb. Minn. Geol. and Pal. Beilb. X, pp. 316, 320.

[2] See op. cit., pp. 281, 359.

cell development known as cœnenchymal gemmation occurs in both, and they are not distinguished.

But Trepostomata generally have *monticules* or maculæ, which Tabulata never have; and therein is the one important distinction. But this also argues their relationship, for the Tabulata, comprising three divisions, can be held as the Paleozoic ancestors and representatives of the Alcyonaria as to three of four divisions respectively, the fourth having no known ancestor, unless the Monticuliporoidea be so considered.[1] Among those of the fourth division *Renilla et al.* show a budding and grouping of the dimorphic zooids similar to or like that which must have obtained in the monticulate *Prasopora et al.* The absence of tabulate skeleton in *Renilla* would be explained as in the case of other Alcyonaria, and need not be recounted here. The supposed relation of Monticuliporoidea and Pennatulidæ I formerly considered as based on deduction and slight evidence, and the explanation of monticules is corroborative.

These same monticules and maculæ, on the other hand, bind the Monticuliporoidea together, *i. e.*, Trepostomata to Cryptostomata. In the preceding paragraphs the relation of Trepostomata to Alcyonarian corals is discussed without the Cryptostomata, but these would not change the argument as given if included. They are generally supposed to be Bryozoa, and are important to that side of the question which will be given later. There is in fact no character in the Monticuliporoidea to separate them from the Tabulata, corals. Their separation, if accomplished, would rest upon stronger evidence binding them to undoubted Bryozoa.

EXPLANATION OF PLATE A

FIG. 1. Monotrypa magna Ulr., cell pattern. × 10.
FIG. 2. Monotrypa magna Ulr., vertical section of cells. × 10.
FIG. 3. Diplotrypa limitaris Ulr., cell pattern. × 10.
FIG. 4. Diplotrypa limitaris Ulr., vertical section. × 10.
FIG. 5. Callopora multitabulata Ulr., a small zoarium, natural size.

[1] Op. cit., p. 349.

FIG. 6. Callopora multitabulata Ulr., *a*) cell in axial region, *b*) vertical of same, *c*) vertical showing peripheral cell region, *d*) cell pattern of peripheral region. × 10.

FIG 7. Prasopora simulatrix Ulr., zoarium, natural size.

FIG 8. Prasopora simulatrix Ulr., cell pattern. × 10.

FIG. 9. Prasopora simulatrix Ulr., vertical section. × 10.

FIG. 10. Batostoma fertile Ulr., *a*) cell pattern × 10, and *b*) surface. × 20, showing mesopore' stabulaæ.

FIG. 11. Eridotrypa mutabilis Ulr. surface × 20, showing calycals. After Ulrich.

FIG. 12. Anolotichia impolita Ulr., cell pattern. × 10.

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MINNEAPOLIS, MINN.,
November 5, 1900.